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Young, D. R. *Effect of food deprivation on treadmill running in dogs.* J. Appl. Physiol. 14(6): 1018–1022. 1959—Effect of food deprivation on endurance capacity was studied in dogs under the following conditions: *a)* 3 and 5 days of fasting with daily high levels of energy expenditure and *b)* 15 days of fasting with low daily levels of energy expenditure. Relative maximum performance, i.e. endurance capacity under conditions wherein work dehydration is a limiting factor, is unaffected by 10–15% body-weight loss and hypoglycemia induced by acute food deprivation. Even with weight loss up to 22%, capacity for daily moderate levels of work is well maintained. Absolute maximum performance (water provided exhaustive treadmill running) improves with 5 days of fasting. Associated with 74% increase in endurance capacity, there is an increased mobilization of body tissue for fuel for the working muscles and a large increase in the post-exercise blood glucose concentration. The dog is resistant to starvation ketosis. In animals tested for absolute performance capacity, the average cumulative calorie deficit, including the exhaustive running trial, was 7500 Calories; yet there was no significant change in the level of blood acetone. It is concluded that absolute performance in the dog increases with 5 days of food deprivation; this response is mediated by a unique permissive effect of such treatment particularly on ability to mobilize body energy reserves.

Recent evidence for deterioration in endurance capacity in man during conditions of acute and semi-starvation (1, 2) is based largely on indirect measures of performance. Particular emphasis has been given to distortions in the cardiovascular and respiratory responses and variations in blood levels of sugar and lactate taken before, during and following a fixed, non-exhausting, work task. Factors tentatively associated with impairment of aerobic work capacity during acute starvation are hypoglycemia, reduction in cardiovascular efficiency, ketosis and associated dehydration. The sequelae to acute food deprivation in man suggest a marked deterioration in performance by the second day of fasting and only slow deterioration thereafter.

In contrast, the picture of work performance in the fasted rat is one of well-maintained or improved physical fitness. Samuels *et al.* (3) have reported a relative constancy in the self-initiated (voluntary) physical activity of rats during food deprivation, followed terminally by a premortal rise in the level of activity. Exhaustive running time, on the other hand, increased markedly during the first 11 days of the fast despite concomitant weight loss and hypoglycemia.

It is obvious from the foregoing examples that we do not yet have a clear picture of the effects of food deprivation on maximum endurance capacity. Experiments with dogs have been undertaken specifically to measure actual maximum aerobic work capacity and variations in the physiological state of fitness in order to establish the relationship between direct and indirect indices of work performance during fasting. To permit comparisons with man, these tests followed the format of human experiments reported above (1).

METHODS

Data presented here have been drawn from a series of experiments conducted with male, pure-bred beagle dogs 18 months of age and weighing 8–12 kg. These dogs had been maintained in a high state of physical conditioning for several months prior to testing. The tests followed a common plan of daily bouts of aerobic work on motor-driven treadmills at 3.63 mph in an air-conditioned (65°F and 50% R.H.) performance laboratory.

In the first series, relative[2] maximum endurance capacity was measured in six dogs after first 3 and then 5 days of fasting. The animals were subjected to the two periods of food deprivation in a random fashion to obviate any potential bias due to the previous period of fasting. Adequate periods of recovery were permitted between fasts. During the test periods daily bouts of running at 10 degrees of inclination were performed by each dog, in an amount equal to 50% of the relative maximum work capacity.

In the second series, absolute[3] maximum performance was measured in two dogs after 5 days of fasting with daily high levels of energy expenditure.

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[1] Publication No. 993, QM Research and Engineering Command, U.S. Army.

[2] Exhaustive running (3.63 mph at 10 degrees of inclination) without water during work.

[3] Exhaustive running (3.63 mph at 10 degrees of inclination) with ad libitum water intake during work.

TABLE 1. *Calorie Deficit, Weight Loss and Relative Maximum Performance Capacity in Six Dogs During Acute Fasting*

	Day of Fasting	
	3rd	5th
Caloric deficit, Cal.	1722±135	3444±269
Loss in body weight, %	8.17±1.26	12.70±2.33
Relative max. performance, Cal.	1205*±193	1224*±261

* Not significantly different from control value of 1191± 211 Cal.

Finally, effects of 2 weeks of food deprivation with low levels of daily energy expenditure on the physiologic responses to a standard 40-minute treadmill test (202.9 kg-m/min.) was tested in four dogs. For these tests, the treadmill inclinations were adjusted for differences in body weight to establish a constant work load at a fixed speed of 3.63 mph. Responses to work of this intensity and characteristics of exhaustive running in the dog have been presented elsewhere (4).

In all experiments the animals were permitted to drink water ad libitum during the periods of rest. In the control phase of testing, calorie requirements for maintenance of weight balance were determined for comparable levels of daily energy expenditure and maximum endurance capacity was measured in the postabsorptive state.

Pulse rate was measured with a cardiotachometer or from a 30-second count from a stethoscope strapped to the chest over the apex of the heart. Readings were taken at 5-minute intervals during the 40-minute period of work, and at 10-minute intervals during the longer running tests.

Body temperature was measured with flexible thermistor probes inserted six inches into the rectum and recording through a multichannel telethermometer.

Oxygen consumption was determined by collection of expired air samples in compensated gasometers and subsequent gas analysis for carbon dioxide and oxygen content in the Haldane apparatus and Beckman oxygen analyzer, respectively. All respiratory volumes were computed for STPD conditions. Caloric expenditure was determined by reference to standard tables for nonprotein R.Q. Respiratory gas exchange during resting conditions was determined from a 6-minute sample of expired air collected while the animals were lying quietly. Gas exchange during the 40-minute period of work was determined from collections in duplicate of 1-minute samples of expired air at 19 and 39 minutes after the start of running; for the longer running trials, 1-minute collections were taken at 1 and 2 hours after the start of running. The exact details for these methods have been presented elsewhere (4–6).

Resting and postexercise blood samples were drawn from the radial vein; aliquots were set aside in heparinized capillary tubes for determination of hematocrit and the rest delivered into fluoridated tubes and immediately frozen for subsequent analyses for glucose (7), lactic acid (8) and acetone (9). In expressing postexercise blood values, corrections have been made for changes in hematocrit after work. the rationale for this procedure has been presented elswwhere (4).

RESULTS

Performance During 5 Days of Fasting With Hard Work

Calorie deficit, weight loss and work capacity. The cumulative decrement in weight and caloric imbalance up to the third and fifth day of fasting is presented in table 1. On the mornings of the 3rd and 5th day of food deprivation, the calorie deficits were computed to be 1722 ± 135 Cal. and 3444 ± 269 Cal., respectively. On the morning of the 5th day the mean body weight loss was 12.70 ± 2.33%. Rate of loss in weight was considerably higher during the early stages of fasting than in the later stages. For the first 2 days, the body weight loss was 8.17 ± 1.26%, whereas for the last 2 days weight loss was 4.53 ± 1.20%. The difference in the means is significant ($P < .01$).

Gross calorie expenditure during exhaustive running was determined from the mean energy expenditure measured after 1 and 2 hours of running multiplied by the total running time. Relative maximum performance, expressed as calories, is presented in table 1. During the control phase of testing, relative maximum aerobic work capacity was 1191 ± 211 Cal. At 3 and 5 days of fasting, the relative maximum capacity was 1205 ± 193 Cal. and 1224 ± 261 Cal., respectively. There is no significant difference in the means.

Absolute maximum working capacity was measured in two dogs. Respiratory gas exchange determined early, midway and late in the course of exhaustive running was substantially similar to the gas measurements made at 1 and 2 hours after the start of running. Aside from the procedure of collecting several samples of expired air and the provision of water during exhaustive treadmill running, the tests and experimental conditions were similar to those described above. During the control phase of testing, absolute maximum work capacity was 2332± 255 Cal.; on the 5th day of fasting and following 10.62 ± 0.21% weight loss, performance was increased to

TABLE 2. *Cardiorespiratory Responses, Water Loss and Body Temperature for Daily Steady State Work* During Acute Fasting in Six Dogs*

	Control	Day 2†	Day 3†	Day 4†
Energy expenditure, Cal.	568	610	601	596
O_2 uptake, cc/kg/min.	54.9 ±8.16	59.9 ±7.66	58.8 ±4.76	55.5 ±4.90
Ventilatory efficiency, cc/l.	12.7 ±2.44	13.9 ±2.29	13.9 ±2.39	13.0 ±3.08
Pulse rate/min.	219 ±7.09	217 ±10.3	205 ±15.9	191 ±14.1
O_2 pulse, cc/beat	2.57 ±0.55	2.64 ±0.64	2.68 ±0.64	2.44 ±0.41
Water loss, cc/Cal.	1.28 ±0.17	.91 ±0.13	.87 ±0.11	.94 ±0.17
Rectal temp., °F	102.9 ±0.94	102.2 ±0.48	102.4 ±0.59	101.9 ±1.02

* Treadmill running at 3.63 mph and 10 degrees of inclination. † Day of fasting.

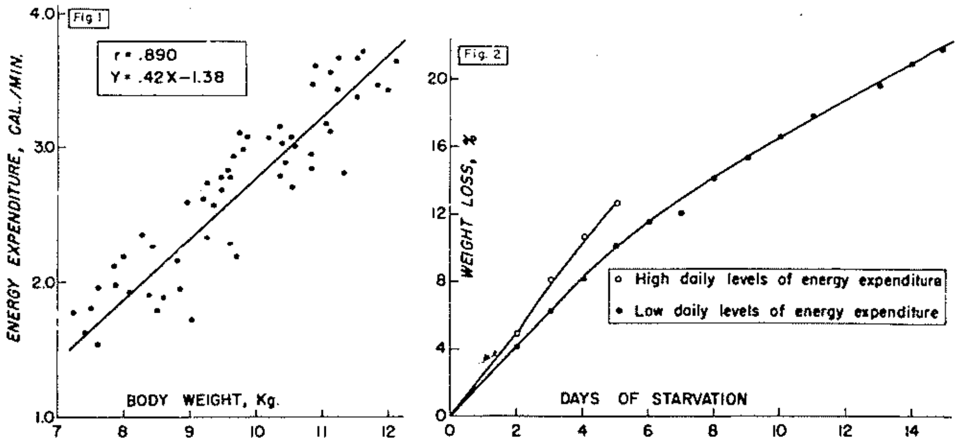

FIG. 1. Relationship between variations in body weight during food deprivation in dogs and energy cost of treadmill running at 3.63 mph and 10 degrees of inclination. Energy expenditure in Cal/min. is shown on *ordinate*. Body weight in kilograms is shown on *abscissa*.

FIG. 2. Average body weight loss during food deprivation. Percentage weight loss is shown on *ordinate*. Days of fasting are shown on *abscissa*. Acute fasting with daily high levels of energy expenditure is denoted by O. Chronic fasting with daily low levels of energy expenditure is denoted by ●.

4056 ± 182 Cal. This 74% increase in absolute work capacity associated with food deprivation and weight loss is highly significant ($P \ll .01$).

Responses to submaximal aerobic work. Physiologic responses to daily bouts of treadmill running at 10 degrees of inclination are set forth in table 2.

Gross oxygen uptake, and the calorie expenditure which is derived from this measure, decreased during fasting. The relationship between caloric cost of treadmill running at a fixed grade and speed and variations in body weight during fasting is set forth in figure 1. The product-moment coefficient of correlation for these two functions is +.890. The linear relationship $Y = .42X - 1.38$ was fitted to the data by the least squares method, where Y is the energy expenditure in calories per minute, and X is the body weight in kilograms. However, when oxygen uptake is corrected for body weight the values are constant; thus the daily work oxygen consumption over the period of testing was 57.4 ± 2.13 cc/kg/min.

Work pulse rate declined during fasting. Mean pulse rate measured during the control period was 219 ± 7 beats per minute; on the 4th day of fasting, the pulse rate was 191 ± 14 beats per minute. The difference in means is significant ($P < .01$).

Water loss during treadmill running was determined from the change in body weight. The water loss in cubic centimeters per calorie expended during work decreased during fasting (table 2). For the control period, water loss was 1.28 ± 0.17; by the 2nd day of fasting the loss was 0.91 ± 0.13 and remained relatively constant thereafter. The difference in the means is significant ($P < .01$).

Ventilatory efficiency and oxygen pulse, which are measures of respiratory and cardiovascular performance, were unaffected.

Metabolic responses to exhaustive running. The respiratory quotient during relative maximum work performance and the blood sugar, acetone and lactate prior to and following such work were measured on the 3rd and 5th day of fasting (table 3).

Work R.Q. was unaffected by fasting. The values for the control period, 3rd and 5th day of fasting were .78 ± .05, .77 ± .02 and .79 ± .06, respectively.

Resting blood glucose decreased on the 3rd day of fasting and was relatively constant thereafter. During the control period, the resting postabsorptive blood glucose was 86 ± 6.0 mg %; on the 3rd day of fasting, resting blood glucose was 72 ± 2.3 mg %. The difference in the means is significant ($P < .01$). Resting hematocrits showed no change; the over-all mean was 43, with a standard deviation of 3.1.

In the control trials, postexercise blood glucose showed a significant ($P < .01$) mean fall of 39 mg %. During fasting, the postexercise blood sugars were more variable, but not significantly different from their respective resting values.

Blood lactate and acetone were unaffected by fasting or physical work.

Beneficial effect of weight loss on absolute maximum performance. It has been indicated that absolute endurance capacity improves with 5 days of food deprivation. Some important responses associated with absolute maximum performance are presented in table 4.

The following comparisons between the responses taken during the control period and on the 5th day of food deprivation serve to elucidate the factors leading to improved performance. For both experimental periods, weight loss while running was a constant fraction of the total energy expenditure so that a 74% increase in performance was associated with a 74% greater loss of body weight. If it is assumed that there is negligible work dehydration when water is provided during exhaustive treadmill running, then ability to perform maximally

TABLE 3. *Metabolic Responses of Six Dogs to Exhaustive Running* on the 3rd and 5th Day of Fasting*

	Control	3rd Day	5th Day
Work R.Q.	.78±.05	.77±.02	.79±.06
Resting blood glucose, mg %	86±6.0	72±2.3	69±7.0
Postexercise glucose, mg %	47±5.6	67±20	64±15
Resting blood lactate, mg %	4.2±2.4	2.3±1.3	2.9±1.8
Postexercise lactate, mg %	4.3±1.2	4.3±1.2	3.8±2.7
Resting blood acetone, mg %	1.4±0.18	2.0±0.70	2.2±0.34
Postexercise acetone, mg %	2.3±0.45	3.4±1.4	2.5±0.84

* Relative maximum endurance capacity.

TABLE 4. *Energy Expenditure, Water Intake, Pulse Rate, Body Temperature, Weight Loss and Blood Chemistry Changes**

	Control	5th Day
Max. energy expend., Cal.	2332±255	4056±182
Water intake, l.	1.56±0.230	3.53±0.297
Body wt. loss during work, %	7.05±1.13	12.3±0.070
Final pulse rate/min.	233±14.6	182±3.61
Final rectal temp., °F	104.5±0.070	103.9±0.240
Δ Blood glucose, mg %	−18.0±17.0	+28.0±5.65
Δ Blood acetone, mg %	+1.8±0.29	+0.60±0.42

* During tests (two dogs) of absolute maximum performance on the 5th day of fasting.

must be related to the mass of body tissue which is utilized as fuel for work. Associated with increased ability to mobilize body energy reserves there is a substantial increase in the blood glucose following exhaustive work.

It is not clear from the data whether improvements in absolute maximum performance are due to a unique permissive effect of inanition or simply related to a reduced physiologic cost of work associated with changes in body weight. In favor of the latter thesis are the similar final rectal temperatures. There is no significant difference between mean final temperatures of 104.5° and 103.9°F ($P > .10$). This suggests an effect of body temperature operating as a limiting factor common in both trials. Since the rate of heat production and heat storage was substantially reduced for work at a fixed speed and grade during food deprivation, it simply may have taken a greater work stress to attain limiting body temperatures. According to this rationale, a treatment which tends to minimize rise in body temperature in the dog during exhaustive work would favor improvement in performance capacity.

On the other hand, we have found, during various control tests, that maximum energy expenditure for work at a fixed speed and grade is unrelated to running time per se or the physiologic variables specifically associated with the factor of weight, i.e. smaller dogs run considerably longer with lower rates of energy expenditure and slower rises in body temperature than heavier dogs of the same age, yet show essentially similar gross calorie expenditures. There is no a priori reason to assume this relationship to be altered during weight loss. Indeed, rank-order correlations between the responses to work and body weight during control and fasting trials indicate a tendency among dogs toward a constant relationship with each other. Accordingly, it is suggested that the large improvement in absolute performance following loss in weight through food deprivation is mediated by a permissive effect of such treatment, particularly on the ability to break down tissue reserves for the working muscles.

Further studies are needed to test these hypotheses.

Performance During 15 Days of Fasting With Low Daily Levels of Energy Expenditure

Body weight loss. Effects of 2 weeks of food deprivation were studied in four dogs. Body weight loss during these trials is presented in figure 2. During prolonged fasting with daily low levels of energy expenditure, the mean body weight loss was 21.9% with very little variation. Daily high levels of energy expenditure, in contrast, resulted in a more rapid decline in body weight. In both curves there is evidence for an exponential relationship, i.e. a reduction in daily weight loss with increased time of treatment.

Resting oxygen uptake, body temperature and pulse rate. Variation in the resting oxygen consumption, body temperature and pulse rate during food deprivation are shown in table 5. The gross oxygen uptake in cubic centimeters per minute decreased in a linear fashion with percentage weight loss. The product-moment coefficient of correlation for these two functions is −.934. Even when corrected for body weight, oxygen consumption showed a significant decrease with progressive weight loss, $r = -.884$.

Along with the decreased oxygen uptake per unit mass of tissue, there was a decrease in the body temperature. The product-moment coefficient of correlation between rectal temperature and percentage weight loss is −.860.

Resting pulse rate showed a high degree of correlation ($r = -.982$) with percentage changes in weight up to 18% loss, but thereafter the pulse was constant.

Responses to a fixed work load. Performance was tested during prolonged food deprivation, utilizing a standard 40-minute period of treadmill running adjusted to a constant work load of 202.9 kg-m/min. In these tests, the calorie expenditure per minute was unaffected by changes in weight. The over-all mean expenditure was 3.39 Cal/min. with a standard deviation of 0.26. Consequently it follows that physical work efficiency was constant over the period tested. The mean work pulse rate was constant at 226/min. (S.D. = ±8.6).

Pulmonary ventilation, ventilatory efficiency, respiratory efficiency and the oxygen pulse were constant.

DISCUSSION AND CONCLUSIONS

The pattern of body weight loss during food deprivation with relatively constant daily levels of energy

TABLE 5. *Correlations Between Average Weight Loss and Resting Oxygen Consumption, Body Temperature and Pulse Rate in Four Dogs During 15 Days of Fasting*

Day of Fasting	0	2	3	4	5	7	8	9	10	11	14	15	r
Body weight loss, %	0	4.03	6.27	8.25	10.04	12.01	14.17	15.42	16.68	17.75	20.89	21.88	
O_2 uptake, cc/min.	91	98	95	74	81	70	63	61	54	55	47	55	−.934
O_2 uptake, cc/kg/min.	8.3	9.2	9.1	7.3	8.1	7.2	6.7	6.5	5.8	5.9	5.3	6.3	−.884
Rectal temperature, °F	101.0	100.9	100.6	100.9	100.7	100.2	100.6	100.2	100.4	100.0	99.4	99.2	−.860
Pulse rate/min.	88	76	77	69	69	62	62	59	55	56	57	57	−.982*

* Based on values up to the 12th day of fasting.

expenditure indicates a marked decline in the body weight in the early phases of starvation followed by a diminution in the rate of weight loss as the treatment progresses. Such changes in weight suggest a large loss of body water early in the course of deprivation. This may be somewhat compensated by the reduced water loss during daily standard bouts of aerobic work.

Resting oxygen uptake and body temperature reflect the loss in body weight, particularly the loss of metabolically active tissue. Gross oxygen uptake as well as the gas exchange per kilogram of body weight decline. The latter suggests a decreasing ratio between active and relatively inert body tissue mass. As is to be expected, the body temperature follows the general decline in metabolic rate.

Resting pulse rate shows a significant decline with weight. This is due to either a direct effect of food deprivation on the heart or factors associated with the circulatory system.

More detailed evidence for changes in the body compartments must await the outcome of further chemical analyses of urine samples collected during the test periods.

Relative maximum performance, i.e. endurance capacity under conditions wherein water is a limiting factor, is unaffected by 10–15% body weight loss. When necessary corrections are made to eliminate a systematic effect of body weight on the responses to treadmill running, there is no evidence of impairment in the cardiovascular and respiratory system. Even up to a 22% weight loss capacity for daily moderate levels of work is well maintained.

Seldom is one in a position to record the absolute potential of an experimental animal. After 5 days of fasting, absolute work capacity increased 74%. One dog when offered water ad libitum during work following the period of fasting ran 140.4 miles uphill without stopping over a period of 38.7 hours. Factors associated with improvements in endurance capacity as a result of weight loss through food deprivation have been discussed. A reasonable explanation is that capacity for physical work is improved through increased mobilization of body energy reserves. Further studies of the biochemistry of starvation are needed to test this hypothesis.

During fasting, the blood sugar level at rest or following exhaustive work is not a reliable criterion of endurance capacity. In the present series, resting blood glucose levels were lowered by food deprivation. Exhaustive work resulting in an energy expenditure of approximately 1200 Cal. did not further change the blood level of glucose. When water was provided during exhaustive running the postexercise blood samples showed a dramatic increase in glucose concentration. These findings suggest that factors other than the blood glucose and extent of caloric deficit limit endurance capacity during fasting.

The dog is remarkably resistant to starvation ketosis. In two animals tested for absolute performance capacity, the average cumulative calorie deficit, including the exhaustive running trial, was approximately 7500 Cal.; yet, there was no significant change in the blood level of acetone. In view of the relatively low work R.Q.'s shown during exhaustive running, it is anticipated that substantial quantities of fat were utilized as a source of energy. Apparently sufficient carbohydrate was available for the complete oxidation of fatty acids via the citric acid cycle.

In general, the animals remained in good temper and were highly cooperative throughout all phases of testing. Emaciation was particularly marked by the increasing prominence of the wing of the ilium and ischial tuberosities. Flank dimensions decreased to the point where the kidneys were easily palpated during examination. The dimensions of the head and snout decreased to the extent that smaller respiratory masks were used to insure adequate fit. Weight lost during short-term food deprivation was replaced in 2–3 days of ad libitum feeding. Following 15 days of deprivation, body weight was replaced in 3–4 weeks of controlled refeeding (*ca.* 1300 Cal/day).

Further studies are needed before extensive comparisons can be made of the effects of short-term food deprivation periods on endurance capacity in man and dog. There is general consensus that hypoglycemia and ketosis are prominent factors contributing to loss in endurance capacity in man during fasting. Dehydration and upsets in ionic balance resulting from excretion of salts of the organic acids may well be the cause of impairment in the cardiovascular and respiratory system in man. Our results with dogs fail to implicate ketosis or any responses to treadmill running which can be considered signs of loss in fitness. Thus we may be dealing with an important species difference. On the other hand, most tests of endurance capacity administered to man during periods of food restriction or deprivation have measured combined effects of water and calorie deficits. For a greater understanding of the debilitating effects of food deprivation on physical endurance in man it is necessary to rule out the limiting effect of water deficits.

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